Italian Botanist 5: 25–30 (2018)
doi: 10.3897/italianbotanist.25.24699
http://italianbotanist.pensoft.net

COMMENTARY

Italian Botanist
Published by Società Botanica Italiana

Was Charles Darwin right in his explanation of the 'abominable mystery'?

Sergio Sgorbati[1], Marco D'Antraccoli[2],
Sandra Citterio[1], Rodolfo Gentili[1], Lorenzo Peruzzi[2]

1 *Department of Earth and Environmental Sciences, University of Milano-Bicocca, Piazza della Scienza, 1/4, I-20126, Milano, Italy* **2** *Department of Biology, Unit of Botany, University of Pisa, Via Derna 1, I-56126, Pisa, Italy*

Corresponding author: *Lorenzo Peruzzi* (lorenzo.peruzzi@unipi.it)

Academic editor: *S. Biondi* | Received 27 February 2018 | Accepted 1 March 2018 | Published 13 March 2018

Citation: Sgorbati S, D'Antraccoli M, Citterio S, Gentili R, Peruzzi L (2018) Was Charles Darwin right in his explanation of the 'abominable mystery'? Italian Botanist 5: 25–30. doi: 10.3897/italianbotanist.5.24699

Abstract

The site and time of origin of angiosperms are still debated. The co-occurrence of many of the early branching lineages of flowering plants in a region somewhere between Australia and the SW Pacific islands suggests a possible Gondwanan origin of angiosperms. The recent recognition of Zealandia, a 94% submerged continent in the east of Australia, could explain the discrepancy between molecular clocks and fossil records about the age of angiosperms, supporting the old Darwinian hypothesis of a "lost continent" to explain the "abominable mystery" regarding the origin and rapid radiation of flowering plants.

Keywords

angiosperm origin, Darwin, abominable mystery, Zealandia, palaeogeography

Introduction

Charles Darwin's "abominable mystery", as reported in the correspondence with Joseph Hooker, Gaston de Saporta and Oswald Heer between 1875 and 1881 (Darwin and Seward 1903), has ended up representing all the unresolved problems regarding the origin and early evolution of angiosperms. Actually, Darwin was not directly interested in the angiosperm fossils, identification of the ancestor of flowering plants, character homology or the evolutionary history of flowering plants, all subjects that since that time

Copyright *Sergio Sgorbati et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

have worried generations of botanists (Friedman 2009). Instead, Darwin was plagued by the sudden origin and fast radiation of angiosperms all around the world in the mid-Cretaceous, an event that was in contrast with his belief of a gradual, slow evolution. To give an explanation to this problem, Darwin speculated about an early, pre-Cretaceous birth and differentiation of flowering plants in a 'lost continent', which was submerged after angiosperm radiation all around the world: "*plants of this great division must have been largely developed in some isolated area, whence owing to geographical changes, they at last succeeded in escaping, and spread quickly over the world*". (letter to O. Heer, 8 March 1875; see Darwin and Seward 1903: 204) or, again, "*I have sometimes fancied that development might have slowly gone for an immense period in some isolated continent or large island, perhaps near the South Pole.*" (letter to J.D. Hooker, 12 August 1881; see Darwin and Seward 1903: 26).

Even if more fossil and molecular data are now available, as yet, it is not possible to determine the site of origin of the angiosperms (Briggs and Walters 2016). In the past, contrasting views have been developed in this regard, placing the site of origin in the Arctic region (Seward 1927), in alpine biomes of northern latitudes (Stebbins 1974), in SE-Asia (Takhtajan 1969), in E-Asia (Sun et al. 1998; Sun et al. 2001), at high boreal latitudes (Hochuli and Feist-Burkhardt 2004), or in unrelated scattered areas from multiple seed plant lineages (see the polyphyletic-polychronic-polytopic hypothesis by Wu et al. 2002). Overall, there is no consensus on the location(s) of angiosperm origin.

However, if we consider the geographic distribution of the 26 early branching angiosperm families (i.e. 'Archaeangiospermae' sensu Stuessy 2010): ANA grade, Magnoliids and Chloranthaceae (see also APG IV 2016), all of them show a distribution including, at least for tiny areas, Gondwanan territories. Overall, 21 early branching families (81%) are found in SW Pacific Gondwanan areas, i.e. New Guinea, E Australia, Fiji, New Zealand, or New Caledonia, with Amborellaceae, Austrobaileyaceae, and Degeneriaceae endemic to these areas (Fig. 1). Moreover, the worldwide maximum concentration of archaeangiosperm families (about 60%) falls in small portions of the NE Australian coast and Papua Nuova Guinea (Fig. 1).

Although current ranges of these families may significantly differ from their past distributions, taken together these data suggest a possible SE Gondwanan origin of the angiosperms. A more general Gondwanan origin was previously hypothesised also by Cronquist (1988), Retallack and Dilcher (1981) and MacDonald (2003). The presence of early divergent lineages (Amborellaceae, Atherospermataceae, Chloranthaceae, and Winteraceae) in New Caledonia, an island re-emerged from Zealandia only ca. 37 million years ago (Ma) after a period of inundation (Cluzuel and Chiron 1998), is not in contrast with this view. There is increasing evidence that the present New Caledonian biota is the product of late Cenozoic immigration events by means of long-distance dispersal from nearby territories (e.g., E Australia, New Zealand, New Guinea). Also *Amborella trichopoda,* the only extant representative of Amborellaceae, became extinct elsewhere after New Caledonia colonization (Pillon 2012; Grandcolas et al. 2014; Nattier et al. 2017).

Luyendyk (1995) first proposed the name Zealandia for a collection of continental fragments between the Australian and Pacific plates (Smith and Sandwell 1997; Stagpoole 2002). In the last two decades, the progressive accumulation of bathymetric, geological,

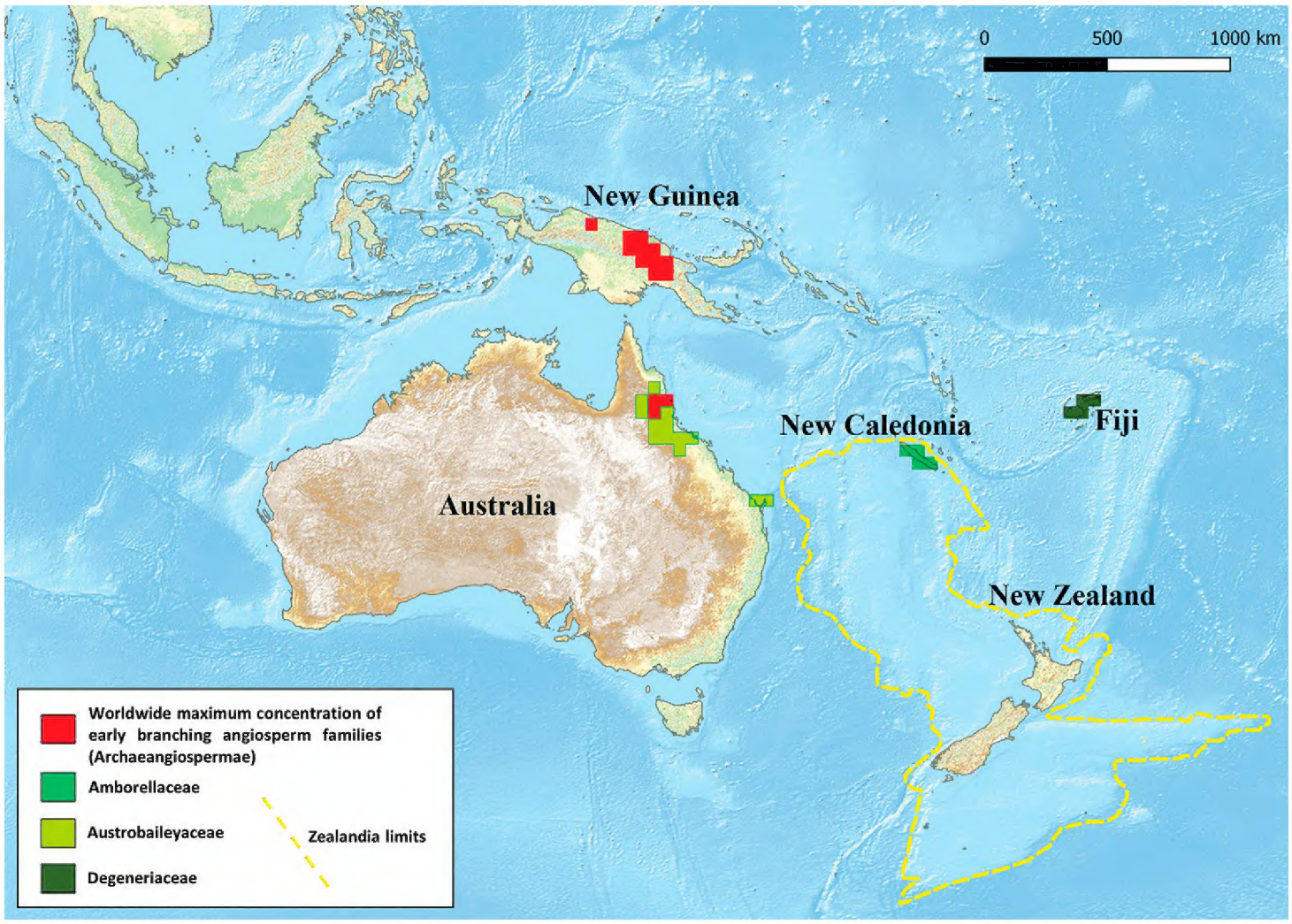

Figure 1. Worldwide maximum concentration of early branching families. Red cells highlight the worldwide highest concentration (15/26, about 60%) of 'Archaeangiospermae' sensu Stuessy (2010). Cells in different tones of green highlight three families (Amborellaceae, Austrobaileyaceae, Degeneriaceae) endemic to New Caledonia, NE Australia, and Fiji, respectively. Zealandia continent (yellow dashed line) is drawn according to Mortimer et al. (2017). The distribution of Archaeangiosperm families was obtained from Angiosperm Phylogeny Website (Stevens 2001 onwards), then georeferenced and superimposed through raster analyses in GIS environment, by means of R software (R Core Team 2017).

and geophysical data, has led Mortimer et al. (2017) to define Zealandia not as a collection of partly submerged continental fragments, but a coherent 4.9 M km^2 continent (Fig. 1), that was formerly part of Gondwana. After its separation from Gondwana (85–130 Ma from Antarctica, 60–85 Ma from Australia; Lewis et al. 2006), Zealandia was 94 % submerged during the late Cretaceous (60–85 Ma; Goldberg et al. 2008).

There is a striking coincidence between the geological evidence of this continent that disappeared in the late Cretaceous and the distribution, around or inside the limits of Zealandia, of many early branching angiosperm families (Fig.1). The age estimates of the divergence of crown group angiosperms using molecular clock data vary considerably, between 140 and 240 Ma or earlier (Martin et al. 1989a,b; Soltis and Soltis 2004; Moore et al. 2007; Bell et al. 2010; Silvestro et al. 2014; Foster et al. 2017). The reconstruction of the genome of the most recent common angiosperm ancestor suggests an age of 214 Ma for its appearance (Murat et al. 2017). By contrast, reliable angiosperm fossil records older than 130–140 Ma have been not found so far (Doyle 2012; Foster et al. 2017, Herendeen et al. 2017). Even though the lack of fossil records before the early Cretaceous suggested to several scholars that angiosperms must have undergone

extremely fast evolution early in their history, Cascales-Miñana et al. (2016) argued that for 100 million years of their evolutionary history angiosperms remained relatively rare, maybe growing in habitats poorly represented in the fossil records. Zealandia was quite a large portion of Gondwana, mostly submerged during the late-Cretaceous (60–85 Ma; Goldberg et al. 2008). This area could have been the cradle of the ancestor and of the early evolution of the main angiosperm lineages during Triassic-Jurassic periods.

Putting the pieces together, our hypothesis is that the flowering plant ancestor could have appeared in the 'lost continent' Zealandia some 200 million years ago or earlier, perhaps from Paleozoic-Mesozoic seed ferns (Taylor and Taylor 2009) after a whole genome duplication event (*Amborella* Genome Project 2013) and/or rapid genome downsizing (Simonin and Roddy 2018), slowly differentiating the main angiosperm lineages (Archaeangiosperms, Monocots and Eudicots) for millions of years. Then, these already established lineages could have spread outside Zealandia, starting from the early Cretaceous, in a rapid worldwide radiation, before its submersion in the late Cretaceous.

In a recent work (Sauquet et al. 2017), the ancestral angiosperm flower was reconstructed. According to these authors, this ancestral flower was bisexual, showing undifferentiated, whorled tepals and stamens with three elements per whorl. This combination of features is not observed in any extant angiosperm, including the earliest-divergent lineages (e.g., ANA grade). If the ancestral angiosperm flower model and our hypothesis are right, we expect that palaeobotanical investigations in the submerged Zealandia region may allow to find (micro)-fossil records showing these putatively ancestral features. Possibly, Darwin's intriguing speculation on the appearance and early evolution of angiosperms in a 'lost continent' was correct.

References

Amborella Genome Project (2013) The *Amborella* Genome and the Evolution of Flowering Plants. Science 342: 1241089. https://doi.org/10.1126/science.1241089

APG IV (2016) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. Botanical Journal of the Linnean Society 181(1): 1–20. https://doi.org/10.1111/boj.12385

Bell CD, Soltis DE, Soltis PS (2010) The age and diversification of the angiosperms re-revisited. American Journal of Botany 97(8): 1296–1303. https://doi.org/10.3732/ajb.0900346

Briggs D, Walters SM (2016) Plant variation and evolution. Cambridge University Press, Cambridge, 600 pp. https://doi.org/10.1017/CBO9781139060196

Cascales-Miñana B, Cleal CJ, Gerrienne P (2016) Is Darwin's 'Abominable Mystery' still a mystery today? Cretaceous Research 61: 256–262. https://doi.org/10.1016/j.cretres.2016.01.002

Cluzuel D, Chiron MD (1998) Upper Eocene unconformity and pre-obduction events in New Caledonia, Comptes-Rendus de l'Académie des Sciences. Science de la terre et de planètes 327(7): 485–491.

Cronquist A (1988) The evolution and classification of flowering plants. New York Botanical Garden, New York, 555 pp.

Darwin F, Seward AC (Eds) (1903) More letters of Charles Darwin. John Murray, London.

Doyle JA (2012) Molecular and fossil evidence on the origin of angiosperms. Annual review of earth and planetary sciences 40: 301–326. https://doi.org/10.1146/annurev-earth-042711-105313

Foster CSP, Sauquet H, van der Merwe M, McPherson H, Rossetto M, Ho SYW (2017) Evaluating the impact of genomic data and priors on Bayesian estimates of the angiosperm evolutionary timescale. Systematic Biology 66(3): 338–351. https://doi.org/10.1093/sysbio/syw086

Friedman WE (2009) The meaning of Darwin's "abominable mystery". American Journal of Botany 96(1): 5–21. https://doi.org/10.3732/ajb.0800150

Goldberg J, Trewick SA, Paterson AM (2008) Evolution of New Zealand's terrestrial fauna: a review of molecular evidence. Philosophical Transactions of the Royal Society B 363: 3319–3334.

Grandcolas P, Nattier R, Trewick S (2014) Relict species: a relict concept? Trends in Ecology and Evolution 29(12): 655–663. https://doi.org/10.1016/j.tree.2014.10.002

Herendeen PS, Friis EM, Pedersen KR, Crane PR (2017) Palaeobotanical redux: revisiting the age of the angiosperms. Nature Plants 3: 17015. https://doi.org/10.1038/nplants.2017.15

Hochuli PA, Feist-Burkhardt S (2004) A boreal early cradle of angiosperms? Angiosperm-like pollen from the Middle Triassic of the Barents Sea (Norway). Journal of Micropalaeontology 23: 97–104. https://doi.org/10.1144/jm.23.2.97

Lewis K, Nodder SD, Carter L (2006) Sea floor geology. Te Ara - the Encyclopedia of New Zealand. http://www.TeAra.govt.nz/en/sea-floor-geology [Accessed 17 January 2018]

Luyendyk B (1995) Hypothesis for Cretaceous rifting of East Gondwana caused by subducted slab capture. Geology 23(4): 373–376. https://doi.org/10.1130/0091-7613(1995)023<0373:HFCROE>2.3.CO;2

MacDonald GM (2003) Biogeography: Introduction to Space, Time and Life. Wiley, New York, 528 pp.

Martin W, Gierl A, Saedler H (1989a) Molecular evidence for pre-Cretaceous angiosperm origins. Nature 339: 46–48. https://doi.org/10.1038/339046a0

Martin W, Gierl A, Saedler H (1989b) Angiosperm origins. Nature 342: 132. https://doi.org/10.1038/342132a0

Moore MJ, Bell CD, Soltis PS, Soltis DE (2007) Using plastid genome-scale data to resolve enigmatic relationships among basal angiosperms. Proceedings of the National Academy of Sciences USA 104(49): 19363–19368. https://doi.org/10.1073/pnas.0708072104

Mortimer N, Campbell HJ, Tulloch AJ, King PR, Stagpoole VM, Wood RA, Rattenbury MS, Sutherland R, Adams CJ, Collot J, Seton M (2017) Zealandia, Earth's hidden continent. GSA Today 27: 27–35. https://doi.org/10.1130/GSATG321A.1

Murat F, Armero A, Pont C, Klopp C, Salse J (2017) Reconstructing the genome of the most recent common ancestor of flowering plants. Nature Genetics 49(4): 490–496. https://doi.org/10.1038/ng.3813

Nattier R, Pellens R, Robillard T, Jourdan H, Legendre F, Caesar M, Nel A, Grandcolas P (2017) Updating the phylogenetic dating of New Caledonian biodiversity with a meta-analysis of the available evidence. Scientific Reports 7: 3705. https://doi.org/10.1038/s41598-017-02964-x

Pillon Y (2012) Time and tempo of diversification in the flora of New Caledonia. Botanical Journal of the Linnean Society 170(3): 288–298. doi: 10.1111/j.1095-8339.2012.01274.x

R Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Retallack G, Dilcher DL (1981) Arguments for a glossopterid ancestry of angiosperms. Paleobiology 7(1): 54–67. https://doi.org/10.1017/S009483730000378X

Sauquet H, von Balthazar M, Magallon S, Doyle JA, Endress PK, Bailes EJ, de Morais EB, Bull-Herenu K, Carrive L, Chartier M, Chomicki G, Coiro M, Cornette R., El Ottra JHL, Epicoco C, Foster CSP, Jabbour F, Haevermans A, Haevermans T, Hernández R, Little SA, Löfstrand S, Luna JA, Massoni J, Nadot S, Pamperl S, Prieu C, Reyes E, dos Santos P, Schoonderwoerd KM, Sontag S, Soulebeau A, Staedler Y, Tschan GF, Wing-Sze Leung A, Schönenberger J (2017) The ancestral flower of angiosperms and its early diversification. Nature Communications 8: 16047. https://doi.org/10.1038/ncomms16047

Seward AC (1927) The Cretaceous plant-bearing rocks of western Greenland. Philosophical Transactions of the Royal Society B 215(421–430): 57–175. https://doi.org/10.1098/rstb.1927.0002

Silvestro D, Schnitzler J, Liow L-H, Antonelli A, Salamin N (2014) Bayesian estimation of speciation and extinction from incomplete fossil occurrence data. Systematic Biology 63(3): 349–367. https://doi.org/10.1093/sysbio/syu006

Simonin KA, Roddy AB (2018) Genome downsizing, physiological novelty, and the global dominance of flowering plants. PLoS Biology 16: e2003706. https://doi.org/10.1371/journal.pbio.2003706

Smith WHF, Sandwell DT (1997) Global sea floor topography from satellite altimetry and ship depth soundings. Science 277(5334): 1956–1962. https://doi.org/10.1126/science.277.5334.1956

Soltis PS, Soltis DE (2004) The origin and diversification of angiosperms. American Journal of Botany 91(10): 1614–1626. https://doi.org/10.3732/ajb.91.10.1614

Stagpoole VM (2002) The New Zealand continent, version 1.0. Institute of Geological and Nuclear Sciences Geophysical Map GPM15.

Stebbins GL (1974) Flowering Plants: Evolution Above the Species Level. Harvard Univ. Press, Cambridge, 480 pp. https://doi.org/10.4159/harvard.9780674864856

Stevens PF (2001 onwards) Angiosperm Phylogeny Website. http://www.mobot.org/MOBOT/research/APweb/, Version 14, July 2017. [Accessed 17 January 2018]

Stuessy TF (2010) Paraphyly and the origin and classification of angiosperms. Taxon 59(3): 689–693.

Sun G, Dilcher DL, Zheng SL, Zhou ZK (1998) In search of the first flower: a Jurassic angiosperm, *Archaefructus*, from Northeast China. Science 282: 1692–1695. https://doi.org/10.1126/science.282.5394.1692

Sun G, Zheng S, Dilcher D, Wang Y, Mei S (2001) Early Angiosperms and their associated plants from Western Liaoning, China. Shanghai Scientific and Technological, Education Publishing House, Shanghai.

Takhtajan A (1969) Flowering plants, origin and dispersal. Oliver & Boyd Ltd., Edinburgh, 310 pp.

Taylor EL, Taylor TN (2009) Seed ferns from Paleozoic and Mesozoic: any angiosperm ancestor lurking there? American Journal of Botany 96(1): 237–251. https://doi.org/10.3732/ajb.0800202

Wu Z-Y, Lu A-M, Tang Y-C, Chen Z-D, Li D-Z (2002) Synopsis of a new "polyphyletic-polychronic-polytypic" system of the angiosperms. Acta Phytotaxonomica Sinica 40(4): 289–322.